Pedobiologia **43**, 64–72 (1999)
Urban & Fischer Verlag

Pedo biologia

Control of leaf litter decomposition rate in a Mediterranean shrubland as indicated by N, P and lignin concentrations

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Accepted: 25. July 1998

Summary. The influence of nitrogen (N) and phosphorus (P) concentration of leaf litter on its decomposition rate was studied for nine Mediterranean shrub and tree species at different time intervals over a two-year period in a Mediterranean shrubland of Southwest Spain. Linear regression between mass loss and the concentrations of lignin, N and P was used to determine the best predictor of leaf litter decomposition during each interval of decomposition. The ratio N to P concentration in leaf litter increased in all species over the period of study, indicating that N is preferentially immobilized as decomposition proceeds. The lignin-to-N ratio was the best predictor of mass loss among the initial chemical characteristics of leaf litter. However, once decomposition started, the lignin-to-P ratio of decomposed material explained mass loss during subsequent intervals better than did the lignin-to-N ratio. When a multiple linear regression was used with the N, P, and lignin concentration as independent variables, the percent of variation in mass loss explained by N concentration decreased over time, while the P and lignin content of leaf litter increased. Our results support the hypothesis of a shift from N-limitation to P-limitation of decomposition rate in the Mediterranean shrublands of SW Spain during the first two years of leaf litter decomposition.

Key words: Nitrogen, phosphorus, lignin, leaf litter decomposition, Doñana National Park, Mediterranean ecosystem

Introduction

An understanding of processes involved in the limitation of productivity is essential for the integrated planning and conservation of ecosystems. Shrubland ecosystems in Southwest Spain are often exposed to recurrent fires, which lead to heavy nutrient losses and, on a long-term basis, a decrease in productivity. Fire volatilizes nitrogen (N), and frequent fires can therefore be expected to lead to N limitations (Vitousek & Howarth 1991). Nitrogen recovery in these ecosystems relies on atmospheric inputs, but high frequencies of fire clearly cause N losses in excess of any replacement by N deposition or fixation. Phosphorus (P) losses by fire are less intense than N losses in these ecosystems, and often P is released into readily available forms after fire (Traboud 1994). Recovery of P relies on the weathering of the bedrock, but P is scarce in quartz parent rock, and quartz chemical reaction is slightly acid, which leads

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0031-4056/99/43/01/64/$ 12.00/0

to moderately low soil pH and forms of P which are not readily available for plants and soil microorganisms (Schlesinger 1997). Nitrogen and phosphorus are the two essential nutrients limiting productivity in these nutrient-poor ecosystems.

In intervals between fires, nutrient availability for plant growth is determined by decomposition and mineralization of litter. Litter decomposition rates are frequently considered to be regulated by substrate quality. In many studies, litter N content, C:N ratio and lignin:N ratio, have been shown to be of critical importance in litter decay (e.g., Melin 1930; Berg & Staaf 1980; Melillo et al. 1982; Taylor et al. 1989). In other studies, P concentration, C:P ratio or lignin:P ratio in litter were shown to influence the decay rate (Heal & French 1974; Schlesinger & Hasey 1981; Staaf & Berg 1982). In the shrubland ecosystems of SW Spain, leaf toughness-to-N and leaf toughness-to-P ratios were the best predictors of litter mass loss (Gallardo & Merino 1993), where leaf toughness was a function of the initial "Klason" lignin content in leaf litter.

Both N and P appear to be important factors regulating leaf litter decomposition rate in Mediterranean shrublands (Gallardo et al. 1997). Differences in the biochemistry of N as opposed to P may be important in order to explain the availability of these nutrients to decomposers and the role of N and P in determining the litter mass loss. Detrital N is mostly carbon-bonded (C-N) and often in structural or complexed forms, while detrital P is mostly ester-bonded (C-O-P) and often soluble. Mycorrhizae, algae, bacteria, and fungi can all produce extracellular phosphatases that cleave the ester phosphate bond (McGill & Cole 1981; Hunt et al. 1983; Howarth 1988). In contrast, multiple enzyme systems are involved in the breakdown of structural or phenolic N-containing organic compounds before any N can be released into available forms. Consequently, N may be relatively less available than P in initial leaf litter. N may be preferentially immobilized in leaf litter by microorganisms, and the N to P ratio may show an initial increase in detritus. As decomposition proceeds, P may become less available than N for decomposers and, at this stage, P content may be the main nutrient controlling the decomposition process.

The objective of this work is to find evidence from correlations to support the hypothesis that increases in the N-to-P ratio leads to a shift from N-limitation to P-limitation of decomposition rate in a Mediterranean shrubland of SW Spain.

Materials and Methods

Area of Study

Our study was conducted in Doñana National Park, Southwest Spain (37°7'N, 6°12'W). Garcia-Novo (1979) and Garcia-Novo & Merino (1993) have presented ecosystem descriptions of the southwestern coast. The area shows the typical winter-wet, summer-dry pattern of a Mediterranean-type climate. Mean annual rainfall of Doñana National Park is ca. 500 mm, with two maxima, one in the winter and another in early spring. Summer drought is severe, with no precipitation during July and August, and little if any during June and September. Mean annual temperature is 16.7 °C. Winter temperatures are mild with a daily mean of 9.3 °C during the coldest months (December and January). Summer temperatures are high, with a daily mean of 23.9 °C for July (the warmest month). More details on the climatic conditions are given in Gallardo (1990). Matorral (scrub) is the predominant vegetation type. The litter bag studies described below were undertaken at a site ca. 20 m above sea level in an open shrubland dominated mainly by *Halimium halimifolium* (L.) Will, *Halimium commutatum* Pau, *Cistus libanotis* L., and *Rosmarinus officinalis* L. Biomass, productivity, and successional changes of this vegetation type are described by Merino & Martin Vicente (1981).

Field methods

Leaf litter decomposition of four shrub species, *Halimium halimifolium*, *Cistus libanotis*, *Quercus lusitanica* Willd. and *Quercus coccifera* L., and five tree species, *Quercus suber* L., *Quercus canariensis* Willd., *Quercus pyrenaica* Willd., *Salix atrocinerea* Brot. and *Fraxinus angustifolia* Vahl. was studied using the nylon mesh bag technique (Bocock & Gilbert 1957). Mesh size was 1 mm, small enough to prevent major losses of the smallest leaves, and large enough to allow free entry of small soil animals.

Freshly abscised leaves of the evergreen species *Halimium halimifolium*, *Cistus libanotis*, *Quercus coccifera* and *Quercus suber* were collected during June 1985, the peak period of litter-fall. Litter from the deciduous species *Quercus canariensis*, *Quercus pyrenaica*, *Quercus lusitanica*, *Salix atrocinera* and *Fraxinus angustifolia* were collected from October to December 1985 from the soil surface. Contaminant debris were carefully picked from each collection, which was thoroughly mixed to provide a uniform leaf litter for each species. The leaf litter samples were air-dried before chemical analysis.

For each species, subsamples of approximately 2 g of air-dried leaf material were weighed to the nearest 0.01 g and placed in 10 × 15 litterbags. Seventy-eight litterbags from each species were distributed randomly on the soil surface in the above-mentioned site at Doñana National Park on 28 January 1986. Between six and ten litterbags of each species were retrieved at bimonthly intervals until January 1988. Litterbags were transported from the field in paper bags to minimize error through spillage (Suffling & Smith 1974).

Analytical and laboratory methods

Litter was dried at 80 °C for 24 h, weighed, and ground to pass through a 1-mm mesh screen. Initial leaf litter subsamples and subsamples from litterbags collected from the field at 2, 4, 8, 12, 16, 20 and 24 months after placement were analyzed separately for N, P and lignin. These data were expressed in concentrations as a percentage of oven-dry biomass. Total N was determined on 0.2 g subsamples using standard Kjeldahl procedures. Phosphorus concentrations were determined in ash using the molybdovanadate reaction (Greweling 1976). The lignin fraction (Klason lignin) was analyzed by sequential analysis of fibre (Robertson & Van Soest 1981). About 1 g of sample was extracted with neutral detergent, followed by acid detergent and 72 % sulphuric acid. Enough replicate samples were analyzed during each procedure of chemical analysis to obtain a coefficient of variation lower than 10 %.

Data analysis

Linear regressions between mass loss of the nine litter types as dependent variable, and lignin, N, P, lignin-to-N ratio and lignin-to-P ratio as independent variables were performed for each mass loss interval longer than six months. Since the lignin-to-nutrient quotients were better predictors of mass loss than were the individual elements, only the results obtained with the lignin-to-N and lignin-to-P ratios were presented. Because lignin, N and P were often partially correlated, we used ANOVA of a stepwise multiple regression (F-to-enter = 4) to select the variables that best explained variation in mass loss at each time interval.

Results

Mass loss values for all time intervals can be found in Gallardo & Merino (1993). Leaf litter mass loss during the first year of decomposition varied between 11.9 % for *Q. suber* leaves and 42.9 % for *F. angustifolia* leaves (Table 1). A narrower range was found in the second year of decomposition, when mass loss ranged between 9.8 % (*C. libanotis*) and 31.4 % (*Q. canariensis*). Lignin and N content for all intervals can be deduced from Gallardo & Merino (1992). Initial lignin content in leaves for the first year of decomposition varied from 8.9 % for *C. libanotis* to 20.1 % for *Q. lusitanica*. The percent of lignin fraction increased for all species, ranging at the beginning of the second year from 19.6 % (*Q. canariensis*) to 36.4 % (*S. atrocinerea*). Initial N content in leaves ranged from 0.33 % (*H. halimifolium*) to 0.93 % (*Q. pyrenaica* and *F. angustifolia*) in the first year and between 0.48 % (*H. halimifolium*) to 1.25 % (*F. angustifolia*) in the second year. Initial P concentration in leaf litter in the first year of decomposition ranged from 300 (g g-1 for Q. lusitanica to 1380 µg g^{-1} for *S. atrocinerea*. Phosphorus concentration decreased by the second year, ranging from 297 (g g^{-1} (*H. halimifolium*) to 549 (g g^{-1} for *Q. pyrenaica* (Fig. 1).

In general, the N-to-P ratio in leaf litter increased over the course of the study. This increase was more pronounced during the first year of study than during the second year, when the N-to-P ratio showed a tendency to remain around a constant value (Fig. 1).

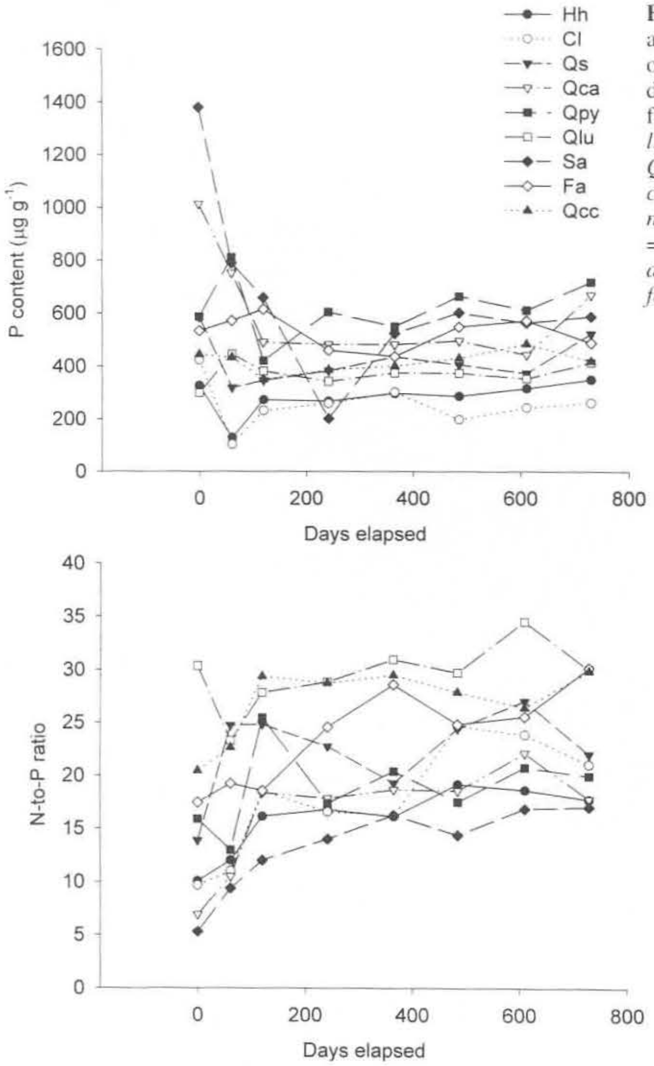

Fig. 1. Changes in P concentration and the N-to-P ratio in several types of litter at Doñana National Park during a 2-yr study. Species codes as follows: Hh = *Halimium halimifolium*, Cl = *Cistus libanotis*, Qs = *Quercus suber*, Qca = *Quercus canariensis*, Qpy = *Quercus pyrenaica*, Qlu = *Quercus lusitanica*, Sa = *Salix atrocinerea*, Fa = *Fraxinus angustifolia*, Qcc = *Quercus coccifera*

Table 1. Mass loss and initial chemical composition (dry mass basis) of the leaves incubated in litter bags at Doñana National Park during the first and second year of leaf decomposition

Leaf litter type	First year				Second year			
	Mass loss (%)	Lignin (%)	N (%)	P (µg/g)	Mass loss (%)	Lignin (%)	N (%)	P (µg/g)
H. halimifolium	12.3	8.9	0.33	328	20.3	26.1	0.48	297
C. libanotis	16.8	8.8	0.41	424	9.8	29.6	0.49	302
Q. suber	11.9	18.1	0.81	585	21.7	21.5	0.84	435
Q. canariensis	21.3	15.6	0.70	1013	31.4	19.6	0.9	482
Q. pyrenaica	26.6	14.3	0.93	587	26.1	20.7	1.12	549
Q. lusitanica	12.7	20.1	0.91	300	18.2	23.4	1.16	375
S. atrocinerea	17.7	18.1	0.73	1380	16.3	36.4	0.85	523
F. angustifolia	42.9	10.5	0.93	533	19.6	19.8	1.25	437
Q. coccifera	18.4	18.8	0.91	445	20.2	22.1	1.18	400

Using simple linear regression models, the lignin-to-N ratio of the initial chemical composition of leaf litter significantly explained variation in mass losses (Fig. 2A). When chemical composition of leaf litter at 2, 4, and 8 months was used to explain variation in subsequent

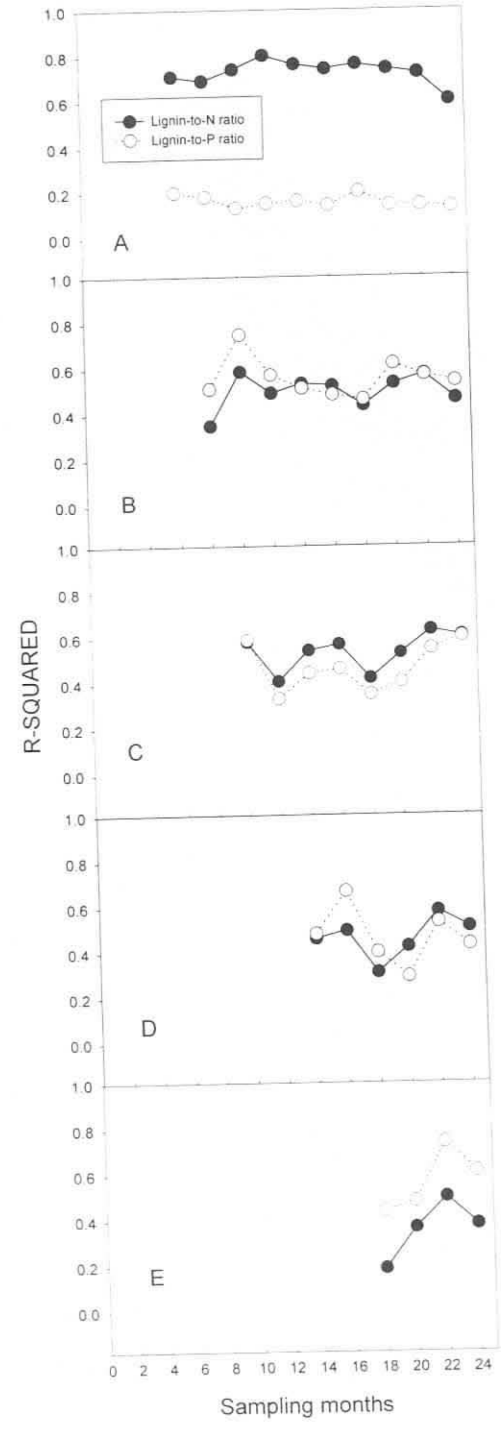

Fig. 2. R-squared resulting from the linear regressions between the lignin-to-N ratio or lignin-to-P ratio as independent variables and mass loss at different time intervals. A: Using initial chemical composition of leaf litter. B: Using chemical composition of leaf litter 2-months old. C: Using chemical composition of leaf litter 4-months old. D: Using chemical composition of leaf litter 8-months old. E: Using chemical composition of leaf litter 12-months old

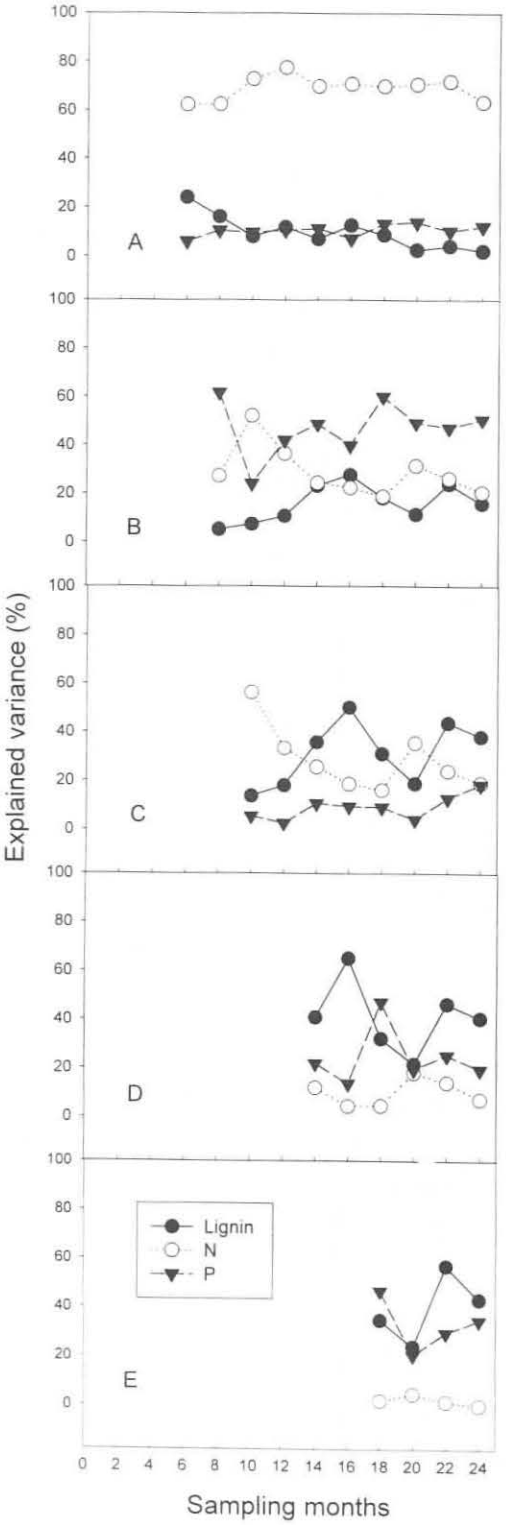

Fig. 3. Proportion of mass loss variance explained by lignin, N and P in a multiple regression model. A: Using initial chemical composition of leaf litter. B: Using chemical composition of leaf litter 2-months old. C: Using chemical composition of leaf litter 4-months old. D: Using chemical composition of leaf litter 8-months old. E: Using chemical composition of leaf litter 12-months old

mass losses, it was found that both lignin-to-N and lignin-to-P ratios explained the variance of the decomposition rate, indicating partial correlation among N and P content of litter (Fig. 2B, C and D). However, only the lignin-to-P ratio of 12-month-old leaf litter was able to explain variation in mass losses during the second year of decomposition (Fig. 2E).

The N content of initial leaf litter explained most of the variation in mass loss (Fig. 3A). However, N content of litter harvested at 2 and 4 months only explained mass loss better than P or lignin in the shortest time intervals (Fig. 3B and C). The percentage of mass loss explained by N declined sharply when chemical composition of 8 and 12 month-old litter was used (Fig. 3D and E). The P content of 2-months old litter explained a higher proportion of variation in mass loss than did N and lignin. As litter progressively decomposed, its lignin concentration explained the greatest percentage of the variation in mass loss, followed by the P content of the litter which had been left to decompose for 8–12 months (Fig. 3).

Discussion

The lignin-to-N ratio of the initial material and the lignin-to-P ratio of decomposed litter were the best predictors of mass losses during the first two years of leaf litter decay. These results are in agreement with the findings of other authors who found that the lignin to nutrient ratio to be the best predictor of litter decomposition rate in a wide range of ecosystems. However, in Doñana ecosystems, Gallardo & Merino (1993) found that leaf litter decomposition is predicted best by the leaf toughness-to-nutrient ratio. Leaf toughness is dependent on the Klason lignin content (i.e., cutin and lignin fractions), but it is also explained by leaf physical characteristics (e.g., spatial distribution of fibre in the cell wall, the linkage between fibre components, and the compaction of fibre). In this work, we could not use the leaf toughness parameter, since measurements of leaf toughness were not possible once the decomposition processes began. The consequence of changes in the composition of a litter during decomposition is that correlations between the rate of mass loss and simple expressions of the initial composition of the litter will have limitations. The correlations subsume a variety of interactions and the later the stage of decomposition the less important are the initial properties of the litter (Heal et al. 1997).

The lignin and N content of leaf litter increased with time. This is likely to be a consequence of the formation of recalcitrant materials (i.e. new lignin-like substances) and of the high rate of N immobilization in litter as decomposition proceeds (Gallardo & Merino 1992). At the initial stages of decomposition, P concentration in litter decreased, and the N-to-P ratio increased. These increases indicate that N was relatively less available than P for microorganisms at the initial stage of litter decomposition when mass losses were regulated by the lignin-to-N ratio. However, the N-to-P ratio values in soil microbial biomass (e.g., Singh et al. 1991; Díaz-Raviña et al. 1993) is lower than the initial N-to-P ratio in the leaf litter types used in this study. Accordingly, it is not easy to explain why N is preferentially immobilized in litter at initial stages of decomposition. We speculate that the way N and P are linked to the organic matter is more important for the availability of both nutrients to the saprophytic microorganisms than the absolute amount of N and P ratio in litter. Initial N content explained most of the variation in mass loss across species during two years of decomposition, but the N content of decomposed leaf litter was unable to explain subsequent mass losses. Initial N is likely to be responsible for determining the initial amount of microbial biomass in litter, which in turn determines the amount of new recalcitrant material (i.e. new like-lignin substances) formed in litter, and the mineralization of P. As decomposition proceeded, N increased and P relatively declined in the litter. As this happened, mass losses became increasingly dependent on the lignin-to-P ratio. The control of the decomposition rate exerted by the N and P concentration in litter suggested that both nutrients are scarce in the Doñana soils, since the activity of enzymes involved in N and P acquisition may be closely tied to the environmental availability of these nutrients (Sinsabaugh et al. 1993; Sinsabaugh & Moorhead 1994).

Our results agree with the model developed by Berg and co-workers (Berg & Staaf 1980; Berg 1984, 1986; Berg & Ågren 1984; McClaugherty & Berg 1987), which found that the first phase of decomposition (<30 % of initial mass loss) is regulated mainly by the nutrient content of litter, while the second phase of decomposition is regulated by the amount of carbohydrates and recalcitrant materials. In our case, although most species lost less than 30 % of their mass during the first year, the variability explained by nutrient content declined from 83.7 % the first year to less than 40 % in the second year. The increase in relative importance of lignin as a predictor of mass loss may indicate that C is increasingly limiting microbial biomass in litter. Further research is necessary to determine if C or P regulate the decomposition rate on a long-term basis in these ecosystems.

Our findings suggested that P limitation prevailed over nitrogen after two years of litter decomposition. Consequently, it may be limiting primary production as well. Apparently, this result disagrees with the model proposed by Walker & Syers (1976) and tested by Vitousek and co-workers (e.g. Vitousek & Farrington, 1997) who proposed a coherent explanation for patterns of soil nutrient availability during long-term soil development. In that model, the weathering of a newly deposited primary substrates (e.g. the dunes of our study) increases the biological availability of P. Nitrogen would be absent in this primary substrate, and must be obtained from the atmosphere by either biological N fixation or atmospheric deposition. Our site may be an exception to the Walker and Syers model based on the reasoning of McGill and Cole (1981). These authors suggested that the greater importance of biochemical mineralization (by extracellular enzymes) of P in comparison to N affects N and P cycling during soil development. Phosphatase activity may be progressively inhibited in our leaf litter as the decomposition proceeds.

These results support the hypothesis of a shift from a N-limited to P-limited decomposition rate in Mediterranean shrubland ecosystems during the first two years of the decomposition process.

Acknowledgements

We thank William H. Schlesinger and three anonymous reviewers for critical comments on the manuscript. The Spanish Ministry of Education and Science financed this work (projects PB 90-0894 and PB 96-0349).

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